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## ***EFFECTS OF VOLUNTARY MOVEMENTS ON EARLY AUDITORY BRAIN RESPONSES***

*S. Makeig  
M. M. Müller  
B. Rockstroh*

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NAVAL HEALTH RESEARCH CENTER  
P. O. BOX 85122  
SAN DIEGO, CALIFORNIA 92186 - 5122

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# Effects of voluntary movements on early auditory brain responses

Scott Makeig\*  
Matthias M. Müller<sup>o</sup>  
Brigitte Rockstroh<sup>o</sup>

\*Naval Health Research Center  
PO Box 85122  
San Diego CA 92186-5122

<sup>o</sup>University of Konstanz  
Department of Psychology  
PO Box 5560  
D-78434 Konstanz  
Germany

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**Abstract**

It has not been clear whether or not early information processing in the human auditory cortex is altered by voluntary movements. We report a movement-related complex event-related potential (CERP) consisting of relatively long-lasting amplitude and phase perturbations induced in an ongoing auditory steady-state response (SSR) by brief self-paced finger movements. Our results suggest that processing in the auditory cortex during the first 50-100 ms after stimulus delivery is affected before, during, and after voluntary movements, beginning with a 1-2 ms delay in the SSR wave form starting 1-2 s before the movement.

**Key words:** EEG, voluntary movement auditory, steady-state, evoked response

## Introduction

Knowledge of cooperative interactions between separate brain regions is crucial to understanding brain and central nervous system function. This report studies the effects of voluntary finger movements on early auditory cortical responses in man. When human subjects are asked to make brief, discrete finger or toe movements at relatively long, self-paced time intervals, a steadily-increasing negative event-related potential (ERP) component appears on the frontocentral scalp 1-2 s before each movement. This so-called readiness or Bereitschaftspotential (BP) (Deecke et al. 1969) is thought to be generated in both primary and supplementary motor cortex (Ikeda et al. 1994). The BP and the ensuing post-movement ERP define a roughly 2 s period during which planning, execution, and updating of psychomotor brain processes relating to discrete movements are manifest. Task-irrelevant auditory, visual, and somatosensory stimuli presented during this period generally evoke smaller responses than when they are presented during rest (Hazemann et al. 1975; Tapia et al. 1987). Several brain loci for these effects have been suggested, including gating of the extralemniscal pathway at the external inferior colliculus (Szczepaniak and Møller 1983) and/or activity in corticocortical inhibitory pathways. But while somatosensory evoked response features as early as 40 ms are modulated by voluntary movements, there has been no consensus that auditory ERP components earlier than P200 (near 180 ms) are affected.

In most auditory gating studies, isolated tones or click probes are delivered at various times relative to experimental events to probe brain responses. Changes in the responsiveness of the central auditory nervous

system to auditory stimulation can also be monitored, continuously and noninvasively, using the auditory Steady-State Response (SSR), a periodic response driven by and phase-locked to a train of periodically-presented brief probe stimuli (Galambos et al. 1981). In adults, the auditory SSR has an amplitude maximum at stimulus repetition rates near 40 Hz (Stapells et al. 1987), and does not habituate so long as subjects remain awake (Galambos and Makeig 1987). It is generally accepted that the auditory SSR is produced mainly by the superposition of middle latency response (MLR) features of the ERP evoked roughly 10-60 ms after each probe train stimulus. Magnetoencephalographic studies indicate that major generators of both the MLR and SSR are located in the bilateral primary auditory cortices (Romani et al. 1982), although additional temporal, subcortical, frontocentral, or widespread generators may also contribute (McGee et al. 1992; Ribary et al. 1991).

Sounds presented occasionally during the SSR stimulus train, or abrupt changes in the train itself, induce perturbations in SSR amplitude and phase that last as long as 2000 ms. Phase-locked 40 Hz-band activity in averaged ERPs to isolated auditory stimulus onsets, here referred to as the auditory *gamma-band response* (GBR) (Makeig 1990; Pantev et al. 1991), lasts only 60-120 ms. Event-related SSR perturbations with longer latencies, therefore, most probably represent modulations of early cortical responses to stimuli in the SSR stimulus train presented *after* the perturbation-inducing event. These SSR perturbations can be measured conveniently in the frequency domain, yielding a complex time series, the *complex event-related potential* (CERP) (Makeig and Galambos 1989; Rohrbaugh et al., 1990) comprised of a series of characteristic deviations in amplitude and response phase that index transitory changes in

the responsiveness of the cortical (and/or subcortical) MLR generators, and/or gating of auditory input to the cortex, presumably produced via subcortical or central arousal pathways (Rajkowski et al. 1994; Hars et al. 1993). SSR phase shifts are equivalent to latency shifts of the entire SSR wave form, positive-going phase advances correspond to latency decreases, and negative-going phase retards, latency increases.

Results of previous CERP experiments involving cued button presses suggested to us that movements themselves may perturb the auditory SSR (Müller et al. *in press*). However, those experiments did not allow separation of cue-related and movement-related response CERP features. We decided, therefore, to test whether an auditory CERP is also produced by voluntary, uncued movements. Results of the study suggest that early stimulus processing in the central auditory nervous system is continuously modulated by both external and internal events. Voluntary movements retard the auditory steady-state response (SSR) by a millisecond or more, first a second or two before a movement, and again a second after it. Immediately after a movement, SSR amplitude is briefly depressed and its latency reduced, these changes resembling a delayed version of SSR perturbations produced by auditory events.

**Materials and Methods***[small print]*

Sixteen right handed subjects (normal hearing, mean age 25 years, 10 female) pressed a button with their dominant index finger at self-paced intervals of about 10 seconds while listening to a continuous train of tones (5 ms, 1000 Hz, 65 dB A-weighted) delivered binaurally via earphones at a rate of 39.25 Hz. Two hundred and fifty button presses were collected from each subject. Before testing, subjects practiced making the required movement several times at ten second intervals cued by the experimenter. During testing, no time-interval feedback was given. Subjects were told to listen to the sounds, and were asked not to count, overtly or covertly, to estimate the 10 s time intervals.

EEG was recorded using Ag/AgCl electrodes referenced to the left earlobe in an analog pass band of DC to 100 Hz, at a sampling rate of 312 Hz, from 3 midline electrodes (Fz, Cz, Pz) and 2 bilateral central sites (C3, C4) of the International 10-20 system, and from 1 cm above and below the left eye. Electrode impedance was brought below 5k $\Omega$  using abrasive skin cleanser. The electromyogram (EMG) was recorded from the thumb flexor muscle (*flexor pollicis longus*) on the right forearm. Before averaging, the influence of eye blinks on the EEG was corrected using a regression procedure (Berg 1986), and epochs containing other artifacts were rejected by visual inspection, leaving on average 79% of the trials available for analysis.

Study of individual trials revealed that the onset of EMG activity had a similar latency (near 200 ms before the button press) in all subjects. Therefore evoked response epochs time locked to the moment of button press were

selected for analysis. EEG epochs of 5 seconds surrounding each button press were first averaged, then the mean baseline (-2.5 s to -1.75 s relative to switch closure) was subtracted from the result, yielding responses that contained ERP components associated with voluntary movements, plus the event-related SSR signal.

The response averages were then lowpass filtered with a 8 Hz cut-off to measure the slow-wave ERP components, while SSR perturbations time locked to the button presses were analysed by complex demodulation. In this procedure, EEG epochs accepted for averaging were first filtered using a (zero phase-shift, 4-pole Butterworth) high pass filter with a 25 Hz cut-off. Averaged epochs were then multiplied by a complex sinusoid at the stimulation rate, and then lowpass-filtered using a zero phase-shift filter with a 5 Hz cut-off. To determine a reliable mean phase during pre- and post stimulus intervals of 500 ms and longer, 2 and 1 Hz lowpass-filtered CERPs were also computed. Finally, CERP amplitude and phase records were derived from the smoothed data.

Four of the 16 subjects were found to have SSR signal-to-noise ratios too low to allow accurate measurement of SSR phase changes, and were omitted from the CERP analysis. A coherent grand mean CERP for the remaining twelve subjects was then computed by frequency-demodulating their grand mean evoked response.

## Results

As expected, the button-press related ERPs at central sites contain an increasing negativity prior to movement onset, the BP, with a steeper negative

slope (NS) period beginning about 500 ms before the button press, larger contralateral to the movement, and followed by the post-motor positivity (PMP at 191 ( $\pm 34$ ) ms after the button press. After normalization by baseline amplitude and phase (Fig. 2a), the movement-related CERP differed very little between the five scalp sites, suggesting they predominantly index the effects of a single SSR modulator system. Analysis of variance on mean amplitude in 500 ms periods indicated that no significant changes in SSR amplitude occurred before the button press, but immediately after it, mean SSR amplitude decreased sharply in 9 of the 12 subjects, reaching on average 49% of baseline at 105 ( $\pm 27$ ) ms ( $F(1,15) = 47.9$ ,  $p<0.001$ ), then rebounded to slightly above baseline (significant at Fz only) near 550 ms. Concurrently, a small (circa 1 ms) but significant phase retard evolved in parallel with the BP at all recording sites (Fig. 2A). Near the button press (and 200 ms after EMG onset), a significant phase advance developed ( $F(1,11)=8.84$ ,  $p=0.01$ ) which peaked during the onset of the post-motor potential. This advance was largest at C3 ( $+30^\circ/-2.1$  ms), contralateral to the movement, and smallest at Pz ( $F(16,176)=3.25$ ;  $p<0.001$ ), and was followed by a sustained phase retard in all channels ( $-17^\circ/+1.2$  ms) beginning near 600 ms post button press.

For comparison with the ERP, the SSR records at all 5 scalp sites were averaged across subjects and converted to CERP amplitude and phase. Fig. 2B superimposes this spatial grand mean on the ERP at the vertex (Cz). Note that: (1) The BP negativity and the CERP phase retard begin together. (2) No notable CERP features accompany EMG onset. (3) The first post-button press peaks in the three records each have different latencies. (4) During the apparent amplitude maximum 600 ms after the button press, SSR phase returns first to

its baseline value, then to its pre-movement retard, which is maintained (in some subjects) to the epoch end.

## **Discussion**

Previous CERP studies have compared responses to various auditory and visual stimuli under various attentional and stimulus expectancy conditions (Makeig and Galambos 1989; Rohrbaugh et al. 1990; Müller et al. in press). This is the first report of a CERP induced by voluntary movement. Our results indicate that early processing of auditory information in the auditory cortex is altered before, during, and after voluntary movements, beginning at the onset of the pre-movement Bereitschaftspotential (BP) and continuing up to 2 s or more after the movement. Although early cortical components of the somatosensory ERP are attenuated by voluntary movements during a period from roughly 100 ms before EMG onset to 500 ms after movement end, interactions have not been demonstrated previously between voluntary movements and auditory ERP components earlier than the N100.

Though the physiological mechanisms that produce the CERP perturbations are not known, four facts strongly suggest that movement-related CERP features reflect changes in the auditory SSR generated during the first 50-100 ms after stimulus onsets: (1) Circa 40-Hz components appear in ERPs to isolated auditory stimuli only during the first 60-120 ms after stimulus onset (Makeig 1990; Pantev et al. 1991). (2) Studies of SSR phase slope as a function of stimulus rate give mean SSR latency estimates near 35 ms (Romani et al. 1982). (3) GBR peaks later than 50-60 ms are small or imperceptible at stimulus rates above one stimulus per second (Makeig 1990; Makeig et al. in

press). (4) The best-fitting single-dipole source location for the magnetic SSR in the auditory cortex is closer to that for the early MLR peak Pa (near 30 ms) than to those for the later peaks of the GBR (Pantev et al. 1993).

The movement-related ERP and CERP do not measure all aspects of movement-related EEG brain dynamics. Voluntary movements are also accompanied by a complex pattern of changes in the spontaneous EEG power spectrum time locked to movement onsets (Makeig 1990), beginning with increases in power at 10, 14, and 19 Hz during anticipation of a movement cue (Pfurtscheller and Araniber 1979; Tiihonen et al. 1989; Kristeva-Feige et al. 1993), followed by increases and reductions in power at various times, frequencies, and scalp locations during movement and movement preparation (Pfurtscheller et al. 1993). In BP experiments, attenuation of 10-14 Hz activity over the cortical region corresponding to the body part being moved begins near the onset of the BP and the CERP phase-shift, and is accompanied by changes at other EEG frequencies including small foci of enhanced 28-40 Hz activity, centered in contralateral dorsolateral prefrontal cortex, immediately preceding the movement. However, like the late portion of the BP (Fig. 1A) and most somatosensory ERP features, movement-related spectral changes are observed mainly contralateral to the movement, while neither the baseline SSR nor the CERP amplitude and phase shifts are lateralized. This implies that the movement-related CERP features are not the result of superposing movement-related 40 Hz-band activity from contralateral somatomotor or adjacent polysensory cortical regions on the SSR by volume conduction (Di et al. 1994).. Event-related changes in middle ear muscles are unlikely to produce the movement-related CERP, since they do not generate the auditory CERP. Rather, the movement-related CERP appears to measure modulations of the

amplitude and latency of the auditory SSR concurrent with or initiated by somatomotor brain activity.

It remains to be determined whether the movement-related CERP is task- and/or modality-specific, and which modulators, pathways, and SSR generators interact to produce it. Although the magnetic SSR is often modelled using a single bilateral pair of equivalent dipole generators in the auditory cortices (Romani et al. 1982; Pantev et al. 1993), our results suggest that activity in more than one source pair generates the movement-related CERP. First, the  $-116^\circ$  midline SSR phase gradient (Fz to Pz) is incompatible with a single pair of bilateral sources. Second, the significant differences in the post-movement phase advance at the different scalp sites suggests that the CERP may sum separate perturbations of SSR response activity generated at more than one central or bilateral source.

The post-movement portion of the movement-related CERP appears similar to CERPs produced by auditory events superimposed on or embedded in the SSR stimulus train (Makeig and Galambos 1989). In both cases, an initial amplitude reduction, accompanied by a phase advance, is followed by an amplitude rebound and a sustained  $\sim 1$  ms latency or phase retard. The onset and peak latencies of these features in the movement-related CERP are roughly 400 ms later than the corresponding features of the auditory CERP (measured from movement and stimulus onset, respectively). The amplitude dynamics of the auditory CERP, in turn, resemble dynamics of visual stimulus-induced gamma band activity in cat visual cortex (Eckhorn et al. 1989), suggesting the action of similar intracortical dynamics and/or similar interactions between

sensory cortex and central arousal systems known to modulate early cortical responses (Rajkowski et al. 1994; Hars et al. 1993).

May some features of the movement-related CERP index changes in subjects' attention within the response epoch? The N1-P2 complex evoked by attended probe tones during a cued warning interval increases during the build-up of the Contingent Negative Variation (CNV), another slow negative-going negative potential which precedes anticipated target stimuli (Rockstroh et al. 1993). The N1-P2 response increase probably indexes an increase in auditory attentiveness before the imperative stimulus. No similar pre-movement amplitude increase occurs in the movement-related CERP. However, middle-latency range auditory response components are affected by selective attention only during highly demanding selective-attention tasks (Woldorff and Hillyard 1991), and effects of selective attention on SSR amplitude have not been reported (Linden et al. 1987). Selective attention to auditory stimuli has also been shown to reduce slightly ( by -45  $\mu$ s) the latency, but not the amplitude, of the frequency-following response (FFR), another and still-earlier and higher-frequency (near 250 Hz) steady-state response generated in the auditory brainstem (Hoormann et al. 1994). As this FFR effect is opposite to the much larger ( $>1$  ms) phase/latency delay in the movement-related CERP, and the two responses have different physiological generators, it is likely that the two phase shifts are independent. Since another equally large phase delay appears in the movement-related CERP beginning 600 ms after movement onset, when subjects' attention is presumably returning to the auditory stimuli, it seems unlikely that either CERP latency change indexes changes in subjects' allocation of attention. However, direct tests of this assumption will require further research.

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**Figure Legends**

**Fig. 1.** **A.** Grand mean evoked response (low pass filtered below 8 Hz) time locked to the moment of button press for 16 subjects at 3 central scalp channels. The vertical line marks the moment of the button press. The lower part of the figure shows the mean rectified EMG record. The ERP Bereitschaftspotential (BP) and negative slope (NS) periods, and the pre- and post-motor positivities (MP and PMP) are labelled. **B.** Mean baseline SSR amplitude and phase for 12 subjects at the three midline and two lateral scalp sites. The SSR is significantly smaller (47%,  $F(2,22)=15.04$ ;  $p=0.001$ ) and delayed (+8.2 ms, -116°) at the parietal site (Pz) relative to the frontal (Fz) but is not lateralized (C3 = C4).

**Fig. 2** **A.** Mean movement-related CERP phase for 12 subjects at the 5 scalp sites, each channel normalized by subtracting its phase baseline. **B.** Grand mean CERP amplitude (*thin trace*) and phase (*medium trace*), computed using complex demodulation of the grand mean response summed over the five recording sites and 12 subjects, superimposed on the grand mean button press-ERP at Cz (*bold trace*) to show the relative timing of the CERP and ERP response features. Ordinates: ERP (potential in  $\mu$ V); SSR-amplitude (change from baseline in  $\mu$ V); response phase (change from baseline phase in degrees, plotted negative-up to highlight similarities).

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